Factors Influencing Productivity of Lakes

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Summary

A number of important inverse hyperbolic relationships exist between the standing crop and productivity of lacustrine biological communities, and mean depth. It is possible that the basis of this relationship is the association of deep lakes with areas of severe relief and high rates of erosion; severe erosion corresponds with low productivity, and subdued erosion with high productivity.

Phosphorus, nitrogen, molybdenum and cobalt are all important in productivity and may exert a limiting or stimulating effect.

The availability of carbon in one or other of several different forms (CO_2, HCO_3^-, $CO_3^=$, and dissolved organic matter) has a significant influence on productivity. The importance of dissolved organic matter as a source of carbon should not be overlooked especially in dilute, bicarbonate-poor waters.

The rate of water renewal has a significant influence on planktonic productivity. Planktonic and benthonic productivity should probably be considered separately—we may not be justified in speaking simply of lake productivity.

(a) Morphology

The biological characteristics of a lake, including productivity, are strongly influenced by the morphology of the lake basin. Several important relationships exist between the standing crop and productivity of lacustrine biological communities, and mean depth (Rawson 1955).

Many of you here are not biologists so I should pause briefly to explain the distinction between standing crop and productivity. By standing crop I mean the amount of living material or biomass existing *at a given instant of time* in a unit volume or area. This is a highly variable quantity; if we visited a lake at the time of a phytoplankton bloom, perhaps in spring or autumn, we would obtain a much higher value for the standing crop of plankton than if our visit had been in winter when no bloom was present. However, if we made regular determinations of standing crop at two-weekly or three-weekly intervals throughout the year we could ascertain a useful average value. Productivity refers to the total amount of living matter produced within a unit area or volume during a certain period of time and is thus a *rate*. Sometimes the period of time is a year, when we refer to annual productivity. Sometimes we speak in terms of the number of milligrams of carbon fixed per day. Many communities that have a high productivity are also characterized by high mean standing crops, but this is by no means universally the case.

Returning to the influence of mean depth on standing crops and productivity we may note firstly that the mean standing crop of plankton expressed as numbers or biomass per unit volume decreases with increasing mean depth in a hyperbolic manner as shown in Fig. 1(a). It is quite possible for an appreciable crop of plankton to occur in an extremely deep lake, and this is the meaning of the 'K' term appearing in the equation in Fig. 1(a). This figure is not true of the mean crop of

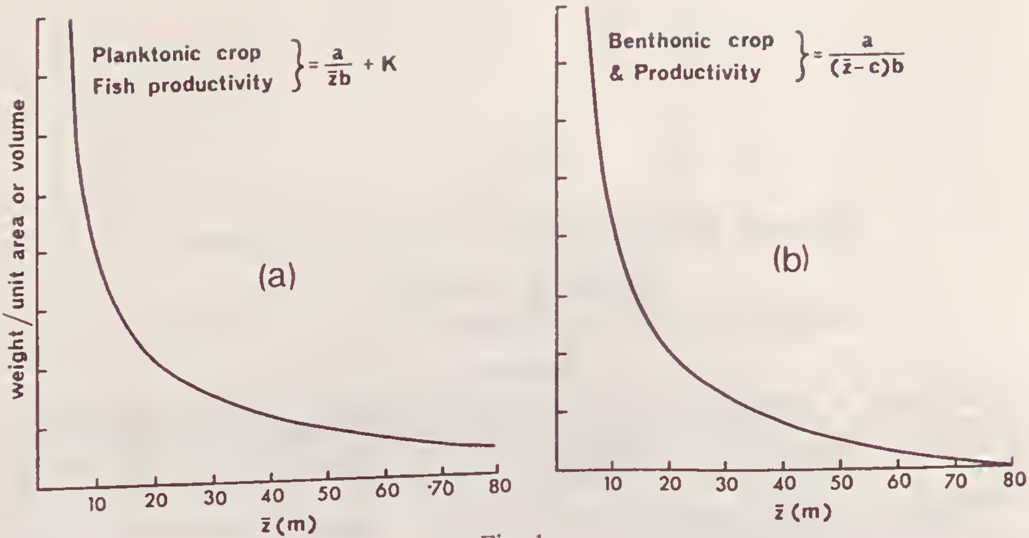

Fig. 1

plankton beneath unit surface area. Considered in this unit there may be very little difference between the planktonic crops or productivity of deep and shallow lakes. There is simply greater dilution of the planktonic material in the deeper lake. Rawson (1955) claimed a hyperbolic relationship with respect to area-based mean standing crop. However, if two somewhat peculiar lakes are eliminated from his plot the relationship is only very doubtfully hyperbolic. The consensus is that planktonic crops expressed in these terms are not clearly or easily related to depth.

Fig. 1(a) will also suffice to show the type of relationship between fish productivity and mean depth. As before there is a 'K' in the equation implying a small but significant production even in very deep lakes. This may be interpreted as productivity based on purely planktonic feeding from the open water region. The relationship between standing crop of fish and mean depth can probably also be represented by an hyperbola. However, information on standing crop is lacking except for very small lakes, and most of the useful data derives from long-term productivity assessed from commercial activity. Since we have no inland fishery of much commercial significance in Australia, such data is derived from overseas, and especially from the Laurentian Great Lakes.

An hyperbola such as that shown in Fig. 1(b) is also a reasonable generalization of the relationship between the mean standing crop of bottom-living organisms and mean depth. On this occasion 'K' is eliminated from the equation, implying that in an infinitely deep lake, if such could exist, there would be a zero crop of bottom-living creatures. In deep lakes with vertical sides, such as Blue Lake at Mt Gambier, this may not be far from the truth. It should be pointed out that the sort of relationship shown in Fig. 1(b) may hold only within a given lake district; if lakes from various parts of the world, or even from different districts of the same country, are considered together this relationship may be obscured because of differences in climate and soil. Although Deevey (1941) and Hayes (1957) doubted the existence of the sort of relationship shown in Fig. 1(b), Deevey (unpublished paper delivered to the AIBS in East Lansing in 1955, and personal communications

1967) now agrees that the sort of relationship between bottom crops and mean depth shown by Rawson (1955) is valid for circumscribed lake districts.

The supply of nutrients to a lake is associated with the formation of soils in the catchment area and the extent to which they are leached (Mackereth 1966). Thus the potential productivity of a lake is influenced by the relative importance of erosion and leaching of soils. A high rate of erosion prevents the production of soils and brings about the deposition of nutrient elements still incorporated in mineral particles in bottom sediments where they are unavailable to lake organisms. Gentle erosion, on the other hand, allows the accumulation of soil in which mineral particles are held in a state that permits leaching to bring the nutrients into solution in a form that is biologically available. A period of severe erosion thus corresponds with low productivity, and subdued erosion with high productivity. Given a particular climate, the productivity of a lake would be partially determined by the topography of the catchment area, since this largely determines its erosional features. It is thus possible that the basis for the inverse relationship between productivity and mean depth is the association of deep lakes with areas of severe relief and high rate of erosion. Shallow lakes are usually found in the flat or rolling country of a mature landscape, whereas deep ones are frequently associated with rugged and broken country.

(b) Phosphorus

Phosphorus is an important constituent of proteins including DNA, and of ADP and ATP which play key roles in energy transfer in biological systems. It is commonly regarded as being more important in determining the amount of living material in a lake than any other single factor (Hutchinson 1957). However, the existence of other almost equally important factors should not be overlooked.

The majority of unpolluted lakes contain from 10 to 40 mg/m^3 of total phosphorus in their surface waters. Where sewage or an appreciable amount of agricultural drainage enters a lake, much higher values for total phosphorus are found, and this is supposed to be the most significant factor contributing to the excessive eutrophy that usually characterizes such lakes.

It is worth pointing out that the addition of phosphate to a lake is probably also equivalent to an addition of nitrate, since phosphate is a nutrient for nitrogen-fixing organisms such as blue-green algae.

(c) Nitrogen

Nitrogen is an important constituent of a wide variety of organic compounds and is especially important in the polypeptide linkage on which the formation of proteins is dependent.

Some nitrate and ammonium nitrogen are present in the atmosphere, and are washed down in small quantities in rain-water. Lightning now appears not to be of importance in forming nitric acid. Appreciable amounts of nitrogen are fixed in the soil by nitrogen-assimilating bacteria, and this not only becomes available for terrestrial plants, but may be leached out of the soils of catchment areas into lakes. In addition, nitrogen-fixing bacteria and blue-green algae are active within the water itself.

From the proteins of living organisms the main decomposition product is ammonia, but in the presence of oxygen this is quickly converted into nitrate by bacteria. Thus in high-oxygen waters unpolluted by human activity, nitrogen is present almost entirely as nitrate and typically in amounts of less than 1 mg/l. In eutrophic lakes, however, the amount of nitrate present is often in excess of 1 mg/l, except in the epilimnion towards the end of the summer stagnation period, and in oxygen-deficient hypolimnia where large amounts of ammonia are commonly present.

(d) Molybdenum and Cobalt

Molybdenum and cobalt are essential constituents of quite a large number of enzyme systems. Molybdenum plays a part in the formation of the enzyme nitrate reductase and is involved in nitrogen fixation. Cobalt is involved in several enzyme systems, and is an essential element in the vitamin B_{12} or cyanocobalamine molecule.

It is known that the amount of molybdenum and cobalt may limit primary productivity since their addition to certain lake waters stimulates photosynthesis (^{14}C measurement) in *in situ* cultures. Goldman (1964) demonstrated this in several lakes in the South Island of New Zealand, and the same is very probably true of many lakes in Tasmania.

On occasion zinc, iron, and manganese can also play a limiting role in primary productivity.

(e) Calcium and the Availability of Carbon

The following classification of lakes on the basis of calcium content has been proposed (Ohle 1934):

$<$ 10 mg/l Ca Poor 10-25 mg/l Ca Medium $>$ 25 mg/l Ca Rich

Some limnologists have tended to assume that calcium content has a major bearing on lake productivity, and have used these designations as if they were productivity terms. The importance of calcium as a limiting factor for freshwater organisms that secrete relatively large amounts of calcium carbonate seems to have been adequately shown. Thus bivalve molluscs are characteristic of hard waters with more than about 20 mg/l of calcium, but are scarce or absent in soft waters with less than about 10 mg/l. It seems, however, that there has been an unjustifiable application of this finding to other groups of animals, for example Crustacea, and from bottom-dwellers to plankton and fish. The inability of freshwater crustaceans to satisfy their calcium requirements when only small amounts are present in the water does not seem to have been adequately demonstrated (Bayly 1964).

Much attention has been paid to the distribution and abundance of higher freshwater crustaceans such as amphipods in relation to calcium. Significant correlations between calcium concentration and the presence or absence of these animals have been obtained. However, since there is a high positive correlation between calcium and bicarbonate in dilute inland waters, similar correlations could also have been obtained with carbonate. In view of the well-established importance of carbon in photosynthesis, and as a basis for organic compounds, it is somewhat surprising that bicarbonate has not been stressed as much, if not more, than calcium. Indeed, in the case of planktonic crustaceans there is some evidence that carbonate and bicarbonate more significantly affect abundance than does calcium (Bayly 1964). Certain alkaline lakes that contain high population densities of planktonic crustaceans contain large amounts of carbonate and bicarbonate but very little calcium. It seems perfectly reasonable to think that large amounts of (bi-)carbonate increase phytoplankton productivity by providing an almost unlimited supply of half-bound carbon dioxide for photosynthesis. In such cases (bi-)carbonate can be considered as having an important indirect effect on planktonic crustacean abundance, especially herbivorous species.

It is not always appreciated that in very low salinity waters ($<$ 100 mg/l) as much, or even more, carbon may be present in dissolved organic matter (D.O.M.

below) as in the form of carbon dioxide and bicarbonate. This, however, enables us to understand the observation that in a series of dilute, bicarbonate-poor lakes varying from clear to dark brown in colour, the abundance of zooplankton is usually greatest in the darkest of the series (Bayly 1964). This is presumably so because of the greater supply of carbon in the latter. The zooplankton in these humified, bicarbonate-poor lakes may be largely independent of phytoplankton for a source of carbon. There is increasing evidence that highly humified waters are characterized by large population densities of bacteria, and that these are of major importance in converting soluble organic matter into cell substance which is then directly available as food for zooplankton.

There seems justification for the view that the availability of carbon, which might be represented in total as $[CO_2 + (HCO_3^- + CO_3^=) + (C \text{ in D.O.M.})]$ is significant in lake productivity, and more so than is calcium.

(f) Salinity or Total Dissolved Solids (T.D.S)

Some limnologists (Rawson 1951, Larkin and Northcote 1958) have pointed out that there is a correlation between productivity and salinity. Basis for this is probably a significant positive correlation between T.D.S. and certain individual elements that have a more fundamental bearing on productivity. It is very doubtful whether salinity *per se* has any fundamental influence on productivity. Nevertheless salinity or T.D.S is fairly easily determined and may be a useful index of productivity where more fundamental data are lacking. In many countries, though not so strikingly in Australia, there is a tendency for high carbonate and bicarbonate values to be associated with high salinity. This being so it would seem that one of the important bases of correlation between T.D.S and productivity is the availability of carbon already discussed.

(g) Water Renewal

The significance of water renewal in a lake will depend on the volume of the lake, the area of the drainage basin, and the amount of rainfall on this area. It will obviously be greatest in a small shallow lake with a large drainage basin receiving high rainfall, becoming less significant the bigger the lake and the smaller the drainage basin and rainfall.

Brook and Woodward (1956) defined, as an index of the rate of water renewal, a *replacement quotient*. This is the volume of water contained in a lake, divided by the amount of water passing out of it during one day. These workers showed that where the rate of water renewal is low, planktonic population densities tend to be high and stable, and vice versa. Ravera and Tonolli (1956), using the less accurate ratio (area of drainage basin): (area of lake), have observed also that as the rate of water renewal increases the planktonic productivity of a lake decreases.

In discussing calcium above I warned against extrapolating from benthonic to planktonic and nektonic communities. Similarly, it is clear that water renewal has a more profound influence on plankton than benthos because outflowing water is likely to be more destructive to drifters than to bottom-dwellers. It would seem, therefore, that we are not completely justified in speaking of lake productivity as if it were monolithic. To be rigorous we should consider planktonic and benthonic productivity separately, although the correlation between the two is probably high.

Addendum

During the discussion that followed the presentation of this paper one questioner pointed out that pH influenced the utilization of molybdenum by blue-green algae and another suggested that pH might have been mentioned as a factor influencing productivity. In reply I pointed out that Hutchinson (1941) doubted whether it had been satisfactorily demonstrated that pH *per se* has any influence on the natural abundance of any aquatic animal with the possible exception of a single protozoan species (*Spirostomum ambiguum*).

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